

SALT AND WATER BALANCE IN LUGWORMS (POLYCHAETA:
ARENICOLIDAE), WITH PARTICULAR REFERENCE TO
ABARENICOLA PACIFICA IN COOS BAY, OREGON

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Polychaetes of the family Arenicolidae, commonly called lugworms, are important members of the infauna of muddy-sand beaches throughout the world, both in estuaries and along the open coast where wave action is slight (Wells, 1963). On suitable beaches, lugworms may be so abundant that their burrowing and feeding activities markedly influence the composition and structure of the substrate (Clay, 1959; Klein, 1967), much as do certain other mudflat polychaetes studied quantitatively by Rhoads (1967). Lugworms are of great importance in processing organic detritus and debris in estuaries (Clay, 1959; Day, 1967; Longbottom, 1970), and provide food for birds (Clay, 1959; Orton, 1925), and bottom-feeding fishes of both sport and commercial importance (Clay, 1959; Day, 1967). Lugworms are therefore a significant link in the detritus food web that is characteristic of estuaries (Darnell, 1967).

Lugworms have been subjects of numerous studies on morphology, feeding and burrowing activities, respiratory physiology, reproduction, and other aspects of their ecology and physiology. Most of these studies have dealt with the common European lugworm, *Arenicola marina* (Linnaeus), while other species of the family have received little attention. These studies have been reviewed several times, initially by Ashworth (1904), and more recently by Wells (1945), Clay (1959), Green (1968) and Krüger (1971). In view of their extensive distribution in estuaries, it is surprising that salt and water balance in lugworms has been so little studied. While there are many separate reports on various aspects of this topic (see Discussion), most of these provide only fragmentary data which do not give a comprehensive picture of any species.

Several species of *Abarenicola* are the common lugworms of estuaries and quiet coastal waters around the North Pacific Ocean from Japan to northern California (Healy and Wells, 1959). *Ab. pacifica* Healy and Wells is one of the most common polychaetes in Coos Bay, the largest estuary in Oregon. Because of the abundance and presumed ecological importance of *Ab. pacifica*, and because of the limited published information on salt and water balance in lugworms generally, the present study was conducted.

MATERIALS AND METHODS

The nomenclature for the Arenicolidae follows Wells (1959, 1963). The abbreviations *A.* will be used for the genus *Arenicola*, *Ab.* for *Abarenicola*, and *Ad.* for *Arenicolides*.

Coos Bay (Fig. 1) is a drowned river mouth of relatively recent geological origin, with a mean high tide area of 10,500 acres, reduced to about 5000 acres at mean low tide. Estuarine effects are detectable about 30 miles upstream in the Coos River system, the only significant source of fresh water to the estuary. In summer and fall, with low river flow, salinities in Coos Bay are high. Salinities lower than 25‰ were not encountered below mile marker 14 in October 1957 (Burt and McAlister, 1959), and below mile marker 10 in summer 1930–32 (U. S. Department of Interior, 1971). In summer 1970, interstitial salinities as high as 28‰ were measured at mile marker 15, in the Coos River. At this time of year the entire Coos Bay estuary is essentially of the well-mixed type (Burt and McAlister, 1959), and complete vertical mixing is further encouraged by tidal over-mixing, a phenomenon which was originally described from this Bay (Burt and Queen, 1957). Only in the channel of Coos River itself is there any vertical salinity stratification (Burt and McAlister, 1959). There are no published records of salinity patterns in Coos Bay during winter and spring when river flow is much greater than in summer. The presence of many stenohaline, sessile marine organisms inside the mouth of Coos Bay, especially on the rocks of Coos Head and near Fossil Point (Fig. 1) suggests that at least the lower portions of the Bay remain dominated by marine water throughout the year.

From the original descriptions by Healy and Wells (1959), and from the ecological and behavioral study by Hobson (1967), one would expect two species of lugworms to be present in Coos Bay: *Ab. pacifica* and *Ab. clapedi* (Levinsen) subsp. *vagabunda* Healy and Wells. However, there are no confirmed reports of *Ab. clapedi vagabunda*. While *Ab. pacifica* was found to be widely distributed and frequently abundant, *Ab. clapedi vagabunda* was not reported in an extensive survey of Coos Bay made by students of the Oregon Institute of Marine Biology during the summer of 1970 (Porch, 1970; U. S. Department of the Interior, 1971). In summer 1970, *Ab. pacifica* was present in nearly all parts of Coos Bay from near the estuary mouth to near the mouth of Coos River at mile marker 15, as well as in a small patch of muddy sand on the marine beach at Sunset Bay (Fig. 1).

For physiological study, lugworms were collected from an extensive intertidal mudflat near Pigeon Point (Fig. 1). Studies by students of the Institute of Marine Biology in the summer of 1969 indicated that circulation patterns in this area were such that the population of worms sampled was seldom exposed to effluent from the pulp mill at mile marker 4. Interstitial salinities were always high, about 95–96‰ of International Normal Sea Water (SW) of 560 mM Cl⁻ (Oglesby, 1969a). Worm burrows were similar to those described for *A. marina* (Wells, 1945) and for *Ab. pacifica* and *Ab. clapedi vagabunda* by Hobson (1967). Densities ranged up to more than 100 worms per square meter. Worms of all sizes were present in the population, ranging from 1–2 cm long up to 8–10 cm in length, weighing over 4 g. The length of the tail portion, relative to the rest of the body, varied considerably, suggesting extensive partial predation by fish or birds, as described by Orton (1925) for *A. marina*.

After collection, lugworms were maintained in non-circulating seawater at 14–16°, without feeding. Glass tubes of appropriate size were provided as artificial burrows, and most worms took up residence in the tubes, performing regular periodic irrigation movements. Lugworms were adapted to various salinities by

stepwise dilution. Experimental media were made with fresh seawater from the laboratory system (salinity 95–96‰ SW) diluted with glass-distilled water. The medium was changed daily to prevent fouling; aeration was not provided. Lugworms were adapted to the test salinity for at least a week before study. The lugworms in 40‰ and 29‰ SW were sampled after only 4 days in the final adaptational medium, since they were in poor condition and it seemed unlikely that they would have survived a full week in such low salinities.

Ten lugworms were sampled at each salinity. Coelomic fluid was taken from the worms as described by Oglesby (1968b) for sipunculids, care being taken to

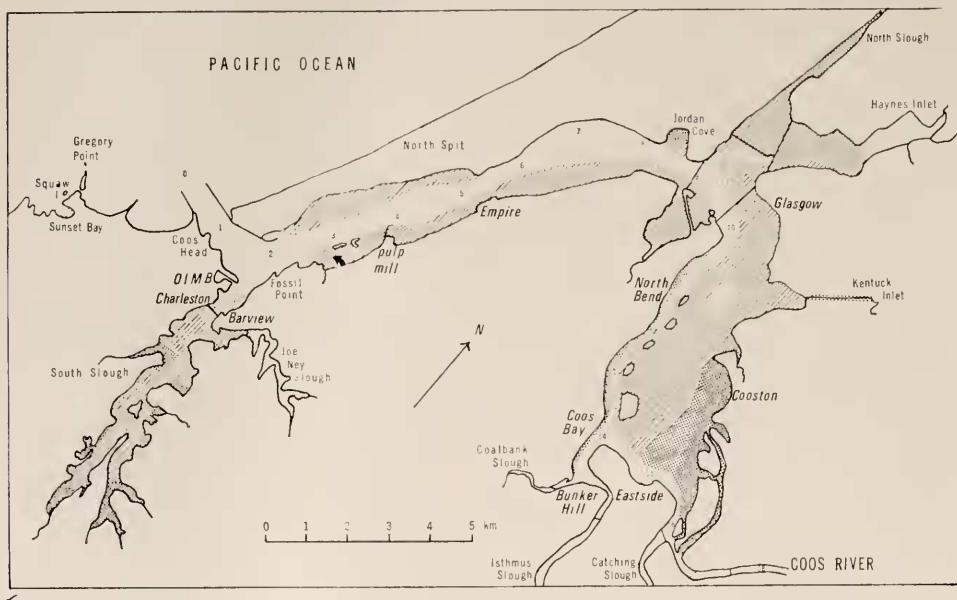


FIGURE 1. Map of Coos Bay, Oregon, showing collecting site for *Abarenicola pacifica* (black arrow). Intertidal areas where lugworms were recorded in 1969–70 are indicated by diagonal lines; intertidal areas of apparently suitable substrate where no lugworms were reported in 1969–70 are indicated by stippling; intertidal areas of unsuitable substrate (coarse sand, rocks, etc.) are indicated by coarse stippling; subtidal areas, and areas not investigated are left blank. Numbers indicate navigation mile markers for main ship channel. Names of towns are italicized.

avoid contamination with gut fluids or blood, and centrifuged to eliminate all cellular material. Measurements of Cl^- were done with a Cotlove chloridometer (Oglesby, 1968b). Measurements of Na^+ were done with an EEL flame photometer (Oglesby, 1970). Osmotic concentrations were measured with a Mechrolab vapor pressure osmometer (Oglesby, 1968b), and expressed as the millimolarity of an equivalent NaCl solution. For water analysis, worms were dried to constant weight.

Results are expressed as the mean ± 1 standard deviation, indicated on the figures by vertical bars. Unless otherwise stated, statistical significance is considered at the 95% level of confidence, using Student's *t*-test.

RESULTS

The osmotic concentrations of centrifuged coelomic fluids of *Ab. pacifica* adapted to salinities from 29‰ SW to 97‰ SW are presented in Figure 2, Cl^- concentrations in Figure 2, and Na^+ concentrations in Figure 3. Coelomic fluid/medium ratios for osmotic, Cl^- , and Na^+ concentrations are presented in Figure 4.

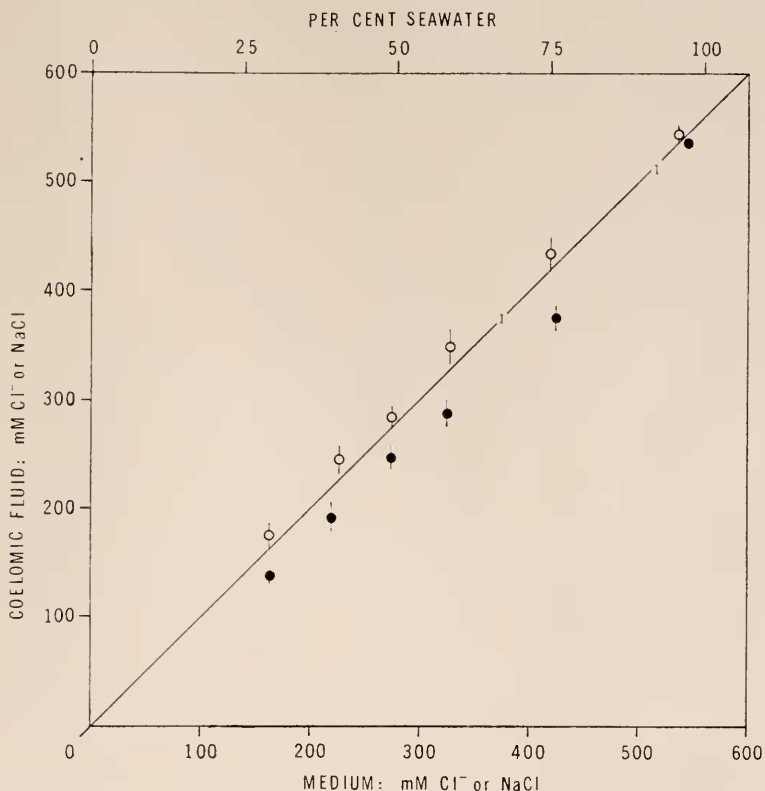


FIGURE 2. Relationship of osmotic and chloride concentration in coelomic fluid of *Ab. pacifica* to Cl^- concentration of external medium. Diagonal line indicates equal internal and external concentration; solid circles, Cl^- concentrations; open circles, osmotic concentrations; Cl^- concentrations for *Arenicola marina*: 1, from Robertson (1949).

The coelomic fluid of *Ab. pacifica* is slightly, but significantly, hyperosmotic to the medium at all salinities tested, by 5.1% ($\text{CF}/\text{M} = 1.05 \pm 0.049$; $N = 60$). There is no indication of increasingly hyperosmotic regulation by lugworms adapted to the lower salinities. The coelomic fluid is slightly, but significantly, hypo-ionic to the medium at all salinities with respect both to Cl^- , by 10.2% ($\text{CF}/\text{M} = 0.898 \pm 0.057$; $N = 60$), and to Na^+ , by 2.9% ($\text{CF}/\text{M} = 0.971 \pm 0.030$; $N = 60$). There are no statistically significant trends in changes of either osmotic or Na^+ concentrations with lowering of external salinity. However, the Cl^- concentration of the coelomic fluid of lugworms adapted to 97‰ SW is

significantly higher ($CF/M = 0.988 \pm 0.010$; $N = 10$) than for the worms adapted to lower salinities ($CF/M = 0.880 \pm 0.044$; $N = 50$). Even in the lugworms adapted to 97% SW, the internal Cl^- was significantly hypo-ionic to that of the medium by 1.2%. There was no significant difference in the extent of this slight hypo-ionic condition between lugworms adapted to 97% SW for 5 days in the laboratory and those adapted for 13 days.

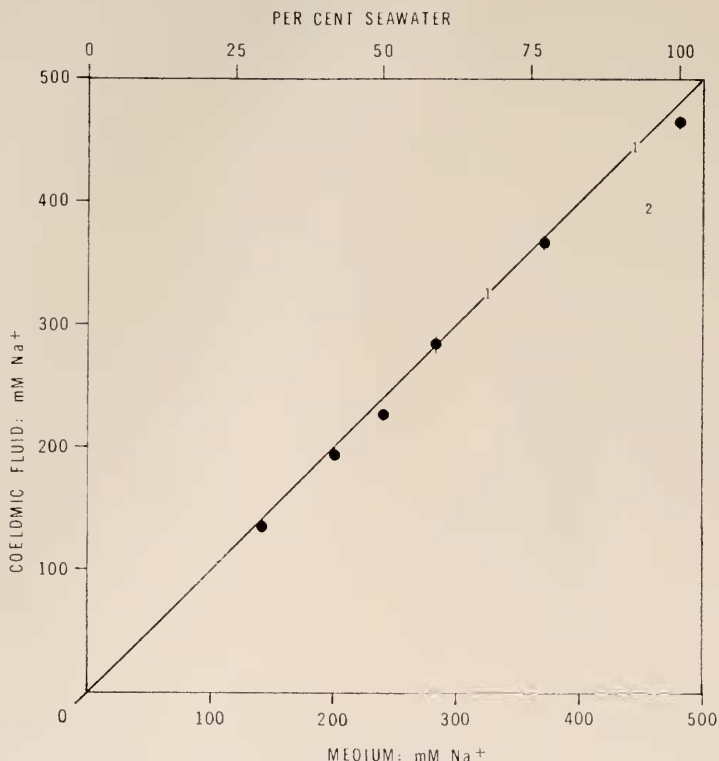


FIGURE 3. Relationship of Na^+ concentration in coelomic fluid of *Ab. pacifica* to Na^+ concentration of external medium. Diagonal line indicates equal internal and external concentration; Na^+ concentrations for *Arenicola marina*: 1, from Robertson (1949); 2, from Nesterov and Skulski (1965).

Figure 5 presents the results of water content determinations of *Ab. pacifica* adapted to a wide range of salinities. A single regression line (method of least squares) was fitted to the data. The results show that the water content of *Ab. pacifica* is strongly dependent upon the external salinity: the lower salinity, the more hydrated the worms become.

DISCUSSION

Abarenicola pacifica is an osmotic conformer over the entire salinity range tested (29% to 96% SW). Over this entire salinity range, the coelomic fluids

are slightly, but significantly, hyperosmotic to the external medium by about 5%. At 100% SW, this would correspond to an osmotic pressure difference of about 1.2 atm., and at 50% SW, to an osmotic pressure difference of about 0.65 atm. While these are the first measurements of osmotic concentration in *Ab. pacifica*, there are several previously published data on two other species, *A. marina* and *Ad. branchialis* (Audouin and Milne Edwards); the available data on osmotic

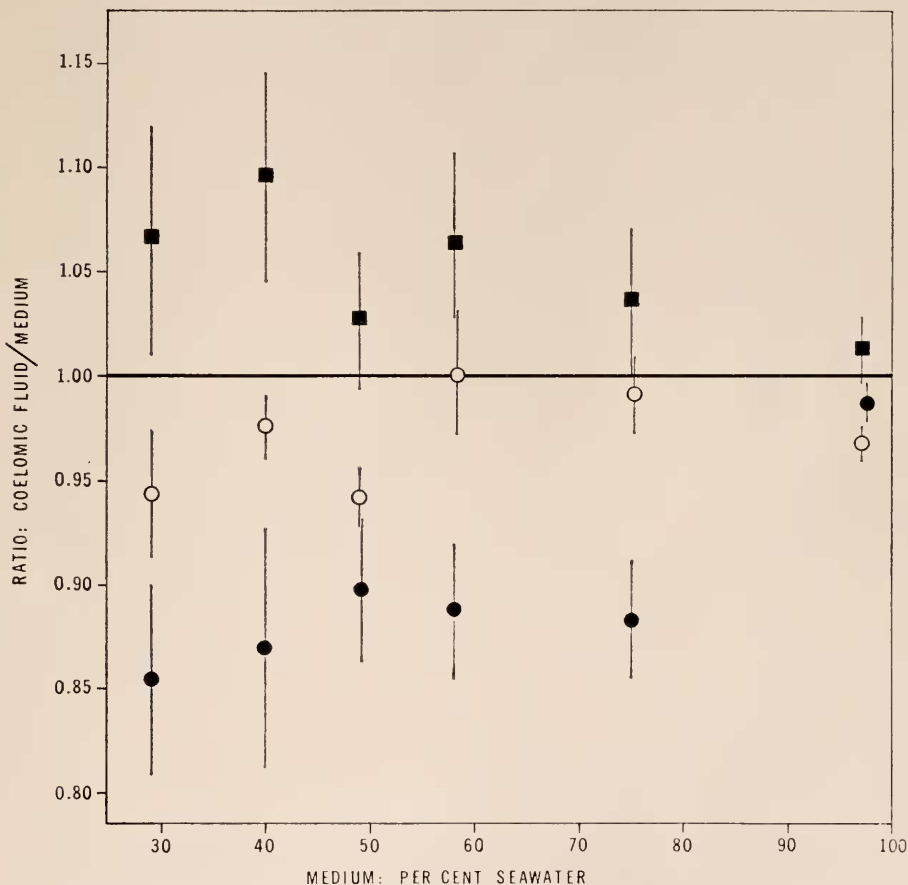


FIGURE 4. Relationships of coelomic fluid/medium (CF/M) ratios for osmotic concentration (solid squares), Na^+ concentration (open circles), and Cl^- concentrations (solid circles) in *Ab. pacifica* to concentration of external medium, expressed as percentage sea water. Horizontal line indicates equal internal and external concentration.

concentrations for all three species are graphed in Figure 6. It should be pointed out that some of these data were obtained for worms which had not been adapted for more than a few hours to experimental salinities. However, in the one study of the time course of changes in coelomic fluid concentrations after a transfer to a lower salinity, Beadle (in Wells and Ledingham, 1940) found that effective isosmoticity was reached in no more than 7 hours by *A. marina*.

The collective data for *A. marina* give the impression that this species is similar to *Ab. pacifica* in being an osmoconformer with the coelomic fluids slightly hyperosmotic to the external medium. The data given by Beadle (in Wells and Ledingham, 1940), Duchâteau-Bosson, Jeuniaux and Florkin (1961), Ginetzinsky (1959), Quinton (1900), and Schlieper (1929) are all within a few per cent of

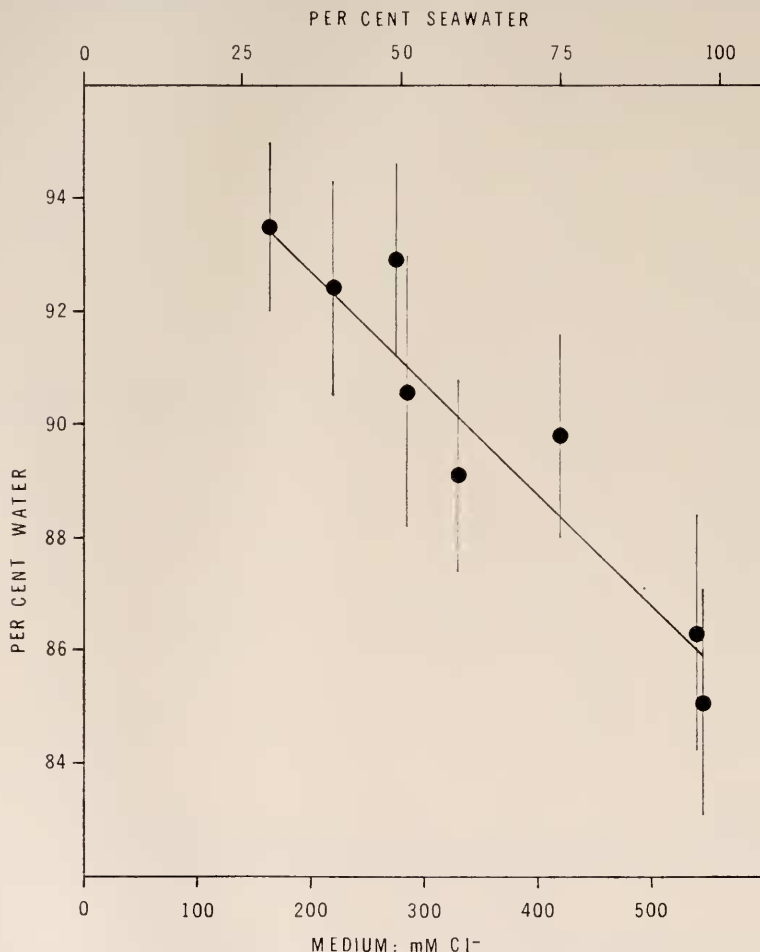


FIGURE 5. Relationship of water content of *Ab. pacifica* to Cl^- concentration of medium.

being iso-osmotic. Primarily on the basis of Schlieper's data, the conclusion that *A. marina* is an iso-osmotic osmoconformer has been repeated in later reviews (e.g. Green, 1968; Krogh, 1939; Oglesby, 1969a; Potts and Parry, 1964). However, Belyaev's (1957) results show a stronger degree of hyperosmoticity, by an average of 9% for the Barents Sea population and an average of 12% for the White Sea population, with some data points ranging as high as 24% more concentrated than the medium. There is some difficulty in interpreting Belyaev's

Figure 9, from which these data were taken, because the freezing point depressions for the media do not correspond to their stated salinity [the relationship, according to Krogh (1939), should be $-1.0^{\circ}\text{C} = 293\text{ mM NaCl} = 18.3\text{‰S}$]. Belyaev's freezing point depression values were taken and regraphed for use in Figure 6.

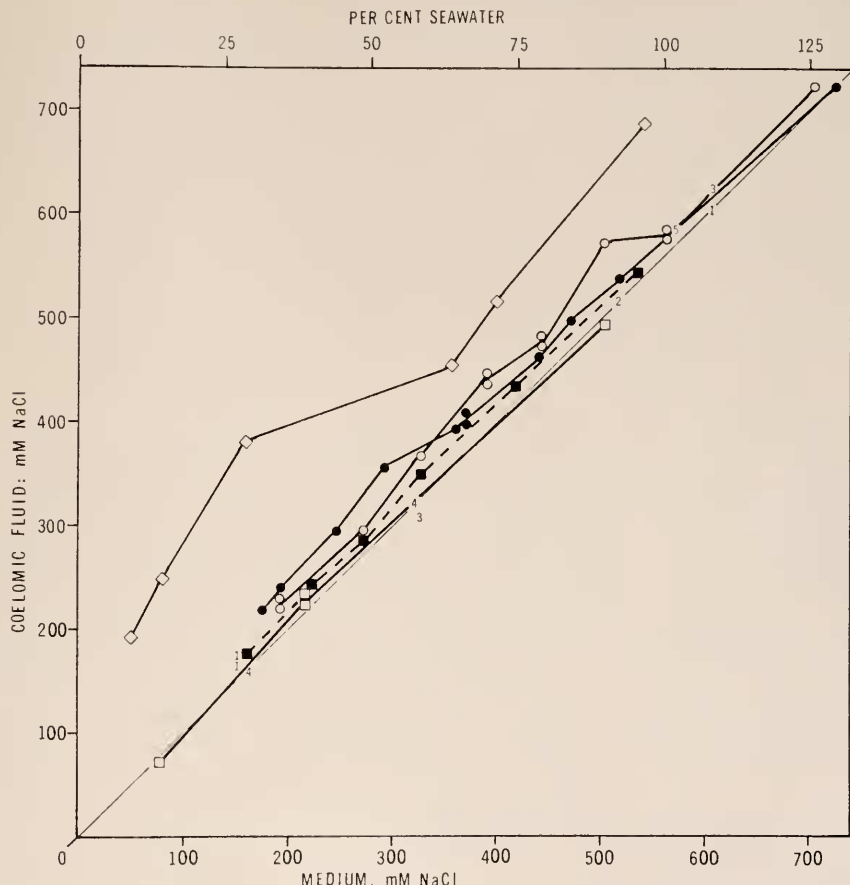


FIGURE 6. Relationship of osmotic concentrations in coelomic fluids of lugworms to osmotic concentrations of external medium: *Arcincola marina*: solid circles, White Sea (Belyaev, 1957); open circles, Barents Sea (Belyaev, 1957); open squares, Kiel and Helgoland (Schlieper, 1929); 1, Plymouth and Bangor (Beadle, in Wells and Ledingham, 1940); 2, Naples (Quinton, 1900); 3, Roscoff (Duchâteau-Bosson, Jeuniaux, and Florkin, 1961); 4, White Sea (Ginetzinsky, 1959); 5, (Krukenberg, in Ashworth, 1904); *Arcicolides branchialis*: open diamonds, Sea of Azov (Zenkevich, 1938a, 1938b); *Abarenicola pacifica*: solid squares, Coos Bay (this report).

Belyaev's interpretation of his results is that both populations of *A. marina* are hyperosmotic regulators at or near their habitat salinities, which were different for the two populations. However, his results as regraphed in Figure 6 do not show any distinct "plateau" of hyperosmotic regulation such as that which characterizes nereid polychaetes (Oglesby, 1969a). Belyaev's results actually seem

more consistent with the conclusion that *A. marina* is a hyperosmotic osmoconformer at all salinities.

Zenkevich's (1938a, 1938b) results for *Ad. branchialis* (as *A. grubei*) present even greater problems for interpretation. As regraphed in Figure 6 (using Zenkevich's data for worms after 25 hours acclimation), *Ad. branchialis* appears to be strikingly hyperosmotic to the medium at all salinities, and shows a marked "plateau" region suggestive of active hyperosmotic regulation between about 25% and 50% SW. Not only are these results different from those for *A. marina* and *Ab. pacifica*, they are different from those for any other polychaete (Oglesby, 1969a). As with Belyaev's Figure 9, the stated environmental salinities in Zenkevich's (1938b) Figure 15 do not correspond to the measured freezing point depressions. Zenkevich (1939b) found marked temporal variations in freezing point depressions after 7, 12 and 25 hours in the experimental salinities, but these variations were not proportional to either the length of the acclimation time or to the salinity. As discussed by Oglesby (1969a), all measurements of freezing point depressions made by Zenkevich (1938a, 1938b) in a wide variety of organisms were markedly hyperosmotic to the "average" environmental salinity in the Sea of Azov. Conflicting data by other workers who have investigated these same or similar species cast doubt on the validity of Zenkevich's results.

It can be concluded, therefore, that both *Ab. pacifica* and *A. marina*, and probably all members of the family Arenicolidae, are osmotic conformers which maintain a slight degree of hyperosmoticity over a fairly wide salinity range. The osmotic behavior of lugworms is thus quite unlike that of many estuarine invertebrates, such as most nereid polychaetes (Oglesby, 1969a), the amphipod *Gammarus duebeni* (Sutcliffe, 1967), and several decapod crustaceans (Gross, 1964), all of which are osmotic conformers only at higher salinities, and are active hyperosmotic regulators at salinities lower than about 25% SW. Rather, lugworms are osmotically similar to the ribbed mussel *Modiolus demissus* (Pierce, 1970), the bay mussel *Mytilus edulis* (Gilles, 1972), and the acorn barnacle *Balanus improvisus* (Newman, 1967), as well as the polychaetes *Nereis virellus* (Oglesby, 1965) and *Cirriformia spirabranchia* (Dice, 1969). All are osmotic conformers and all can tolerate a wide range of external salinities; this tolerance permits at least some to penetrate far into the oligohaline reaches of estuaries.

It has only recently been realized that many marine and estuarine animals, usually considered to be iso-osmotic, in fact maintain a small but statistically significant degree of hyperosmoticity of the body fluids to the environment (Dice, 1969; Pierce, 1970; Renmurt, 1969), as was remarked upon as long ago as 1935 by Nicol. Pierce (page 530) believes that "any animal having protein in solution in its extracellular water and permeable external membranes must be hyperosmotic to its environment," this condition being the purely passive consequence of the presence of osmotically active but indiffusible particles such as proteins in the body fluids resulting in a Gibbs-Donnan equilibrium. Pierce (1970) suggested that the usually small differences in osmotic concentrations between the body fluids and the external media had hitherto gone unrecognized because earlier workers had used less precise methods than are now available. Pierce's conclusion, while theoretically attractive, may not be true for all real animals, even when one excludes from consideration such hypo-osmotic regulators as marine teleost fishes, many crabs, and the brine

shrimp *Artemia*. Most sipunculid worms, for example, seem clearly to be iso-osmotic conformers at all tolerable salinities (Oglesby, 1969a; Hogue and Oglesby, 1972). The one reported measurement of plasma protein concentrations in lugworms is only 0.2 g/l (in *A. marina*: Robertson, 1949), a value at the low end of the range of plasma protein measurements in body fluids of those worms lacking a dissolved respiratory pigment (Oglesby, 1969a). Robertson (1949) carried out dialysis experiments of body fluids against sea water using collodion membranes, and concluded that a Gibbs-Donnan equilibrium was not significant in many marine invertebrates, including *A. marina*.

Remmert (1969, page 424) offered no explanation for his conclusion that "osmotic conformers are slightly hyperosmotic in their normal environment." Pierce (1970) discussed aspects of the differences in osmotic pressures between blood and pericardial fluids in bivalve molluscs, but did not address himself to the ecological role, if any, of the blood's being hyperosmotic to the external environment. Dice (1969) suggested that the maintenance of hyperosmotic coelomic fluids in marine annelids caused a constant osmotic influx of water into the worm which could replace water lost in the urine. Strunk (1930a) and Chapman and Newell (1947) have described fairly copious urination by *A. marina*, so the necessity for replacing urinary water is present. Dice's (1969) suggestion seems quite likely as at least a partial explanation for the adaptive value of slightly hyperosmotic body fluids in marine and estuarine osmoconformers.

Na^+ and Cl^- concentrations are slightly lower in the coelomic fluids of *Ab. pacifica* than in the external medium at all salinities, by about 3% and 10%, respectively (Figs. 2, 3). In the case of Cl^- , the CF/M ratio was significantly lower in worms adapted to salinities below the habitat salinity of 97‰ SW. Robertson (1949) and Nesterov and Skulski (1965) have measured Na^+ in the coelomic fluids of *A. marina*, and Robertson has also reported values for Cl^- ; these are indicated by small numbers in Figures 2 and 3. Robertson's data indicate that this species has coelomic fluids that are virtually iso-ionic with respect to both Cl^- and Na^+ , and that this situation does not change after a short exposure to lowered salinity. On the other hand, Nesterov and Skulski's measurement of Na^+ is 14% lower in the coelomic fluid than in the medium.

Bialaszewicz (1933) gave data for several ions, including Cl^- but not Na^+ , in the coelomic fluids of *Ab. clapedi*. Since he did not report the ionic composition of the external medium (about 112‰ SW), it is not possible to compute exact CF/M ratios for any of the ions he measured. The ratios discussed below were calculated on the assumption that the coelomic fluids of *Ab. clapedi* are iso-ionic with respect to Cl^- (see Oglesby, 1969a).

Bialaszewicz (1933), Nesterov and Skulski (1965), and Robertson (1949) have reported on several additional ions in *A. marina* and *Ab. clapedi*. Among the cations, K^+ was reported by all three workers to be hyper-ionic in both species, by 2.5–39.7%. Robertson observed that the CF/M ratio for K^+ increased from 1.035 to 1.18–1.20 after *A. marina* had been briefly exposed to about 50‰ and 67‰ SW. (But see Oglesby, 1970, and Hogue and Oglesby, 1972, for critical discussion of the significance and reliability of apparently elevated K^+ concentrations in worm body fluids.) The reported value of 0.0214 mM Li^+ for *A. marina* (Nesterov and Skulski) suggests that this ion is present in the coelomic fluid at

about 1.5 times the concentration in normal seawater. Ca^{++} is reported to be 0.2% lower in the coelomic fluid of *A. marina* than in the medium (Robertson), but 17.2% higher in *Ab. clapedi* (Bialaszewicz). Again, Robertson observed that the CF/M ratio for Ca^{++} rose from 0.998 to 1.12–1.13 after the worms were exposed to 50% and 67% SW. Mg^{++} was reported to be 0.3% higher in the coelomic fluid of *A. marina* than in the medium (Robertson), but 0.9% lower in *Ab. clapedi* (Bialaszewicz). Both Bialaszewicz and Robertson found somewhat reduced SO_4^- concentrations (8.2% and 7.8%, respectively). Robertson's dialysis experiments showed that CF/M differences for K^+ and SO_4^- were not the result of Gibbs-Donnan effects caused by the presence of proteins. It cannot be stated whether the differences between Bialaszewicz's and Robertson's measurements for most of these ions represent valid specific differences, or whether they are the result of different analytical methods. In none of these studies was the statistical significance of the slight deviations from iso-ionic conditions evaluated.

Taken together, these data do not indicate any marked ionic regulation in lugworms. However, some of these aniso-ionic situations, though slight, may be real; for example, Cl^- and Na^+ in *Ab. pacifica*, and K^+ and SO_4^- in *Ab. clapedi* and *A. marina*. With the exception of K^+ , the concentrations of these ions in the coelomic fluids are lower than in the external medium, even though the coelomic fluids are hyperosmotic to the medium. This suggests the presence of an ion deficit in the coelomic fluids of lugworms, particularly marked for anions, which is perhaps made up with organic, or nitrogenous substances, or both.

There have been very few measurements of organic substances in the body fluids of any worms (Oglesby, 1969a), and almost none among lugworms. It is reported that *A. marina* has from 0.25–1.83 mM urea (Strunk, 1932), only 0.00059 mM uric acid (Strunk, 1930b), and 0.67 mM glucose and other reducing sugars (Florkin, 1936). Allantoic acid was detected, but not quantified, in coelomic fluid of *A. marina* (Florkin and Houet, 1939). More extensive data are given by Clark (1968a, 1968b) for *Ab. pacifica*. She reported 0.48 ± 0.15 mM NH_3 , and gave 12 pooled measurements for free amino acids (FAA) for worms in three different salinities, for different periods of adaptation to these salinities, and for different portions of the body. For all groups of worms in all salinities, the average value was 10.18 ± 4.98 mM FAA. There were no significant differences between the worms in 100%, 75%, and 50% SW ("100% SW" = 30–32‰ Salinity), for either 1 or 4 days adaptation. The highest single value, 19.78 mM FAA, was the one measurement of coelomic fluid from the tail region, all other measurements being from the trunk. These FAA values are much lower than those Clark reported from many other polychaetes in the same study, which ranged up to 100 mM FAA in the terebellid *Thelepus crispus*. Clark (1968a) also observed differences in pH between the coelomic fluids of tail and trunk regions of *Ab. pacifica*. Using pooled samples from 7 worms, she found the tail coelomic fluid had a pH of 7.49, but that the coelomic fluid from the trunk had a lower pH, 7.30. These values compare well with the only other reported pH measurement for a lugworm, 7.43 ± 0.059 in *Arenicola cristata* Stimpson (Mangum and Shick, 1972).

Adding up all these separate values for both species, 22.76 mM can be accounted for by organic and nitrogenous molecules if Clark's maximum value for FAA in

Ab. pacifica is used, and only 13.16 mM if Clark's average value is used. Such low concentrations could contribute only 1–2% to the total osmolarity in *Ab. pacifica* adapted to 100% SW, and thus are not sufficient to make up the entire difference between the osmotic and ionic concentrations in the coelomic fluid of this species. Some additional osmotically active substance(s) must therefore be present in the coelomic fluids of lugworms.

Ab. pacifica increases markedly in water content when adapted to salinities lower than 97% SW (Fig. 5). For example, a lugworm with 14.4 g solid material (dry weight) would have 85.6 mg water when adapted to 100% SW, but would have 135.8 mg water when adapted to 50% SW, representing an increase of 159% over the water content of the lugworms in the higher salinity. If this lugworm could be adapted to as low a salinity as 25% SW, the 14.4 mg solid material would be associated with 228.6 mg water, a 267% increase in water content over the worms adapted to 100% SW. This dependency of water content upon external salinity is at least as strong as in *Nereis vexillosa* and *Themiste dyscritum*, both species with a far less extensive distribution in estuaries (Oglesby, 1965, 1968b, 1969a). In an analysis of water-content regulation in various worms (Oglesby, 1973), it is shown from the present data that *Ab. pacifica* retains about 65% of the excess water which would be taken up osmotically by a theoretical "perfect osmometer" after transfers to lower salinities; even *T. dyscritum* is capable of preventing the retention of more of this excess osmotic water than *Ab. pacifica*. These observations on steady-state water content regulation are supported by visual observations of extensive swelling associated with transfers of lugworms to lower salinities, accompanied by distention and even breakage of the body wall. Swollen worms were incapable of making normal ventilatory movements, and would be expected to have difficulty in burrowing. Below 50% SW, these abnormal responses were especially noticeable.

Very few investigators have addressed themselves to the problem of water regulation in lugworms, and what information exists was obtained quite incidentally to other studies. There have been several reports of water content in *A. marina* and *A. cristata* (see Table I, Oglesby, 1969a), and although all worms were probably taken from approximately full-strength seawater, in no case was the external salinity indicated. The reported values have an extraordinary range, from 78.6% to 97.0% water just for one species (*A. marina*). Both extremes are well outside the range of water content in all salinities reported here for *Ab. pacifica*. Probably these data should be used with caution until more carefully controlled work is done with *A. marina*.

The tendency for a worm to approach its initial weight after a transfer from one salinity to another is termed "volume regulation" (Oglesby, 1969a). No studies have been published on the actual time course of weight changes after transfers, but scattered comments in the literature indicate that *A. marina* (Dakin, 1908; Ginetzinsky, 1959; Quinton, 1900; Reid, 1929), *Ad. branchialis* (Zenkevich, 1938a); and *Ab. pacifica* (Clark, 1969b; this report) have little or no capacity for volume regulation, suggestions which are consistent with the great variation in steady-state water content observed in *Ab. pacifica*. It can reasonably be concluded that lugworms have a very limited capacity to regulate water content when exposed to variations in environmental salinity.

The studies just discussed indicate that both *Ab. pacifica* and *A. marina*, and very likely all lugworms, are hyperosmotic osmoconformers which cannot regulate volume and water content to any significant extent. When maintained in salinities lower than about 50‰ SW in the laboratory, lugworms are rendered incapable of such vital physiological activities as burrowing and burrow ventilation. Yet *Ab. pacifica* has a very extensive distribution in the Coos Bay estuary, which has some freshwater inflow at all seasons, and very strong freshwater inflows from the Coos River during the rainy season (November–May). Similarly, *A. marina*

TABLE I
Tolerance of low salinities by lugworms

External concentration mm Cl ⁻	Remarks and references
<i>Arenicola marina</i>	
50	Survival only "for a short time" (Reid 1929).
80-85	Serious injuries occur below this level (Khlebovich 1969); survived 26 hours in laboratory (Schlieper 1929).
125	Lowest temporary salinity at which worms were found in field (Nicol 1935); lowest salinity for worms in field (Green 1968; Krogh 1939; Wells and Ledingham 1940).
140-193	Survived only 2 hours in laboratory (Pearse 1928); survived 7 hours in laboratory (Beadle in Wells and Ledingham 1940); no tolerance of lower salinities in laboratory (Belyaev 1957; Ginetzinsky 1959; Sveshnikov 1963).
230	Lowest salinity permitting normal burrowing (Reid 1929).
344-392	Lowest salinity for worms in field (Percival 1929; Popham 1966; Robertson 1949).
<i>Arenicolides branchialis</i>	
48	Survived 25 hours in laboratory (Zenkevich 1938b).
357	Average environmental salinity (Zenkevich 1938b).
<i>Abarenicola pacifica</i>	
162-220	Poor survival in laboratory (this report).
247-277	Survived 4 days in laboratory (Clark 1968b); moderate survival in laboratory (this report).
400	Lowest interstitial salinity at which worms were found in field (this report).

is generally regarded as a typical inhabitant of estuaries in northern Europe (*e. g.*, Green, 1968). In view of their relatively poor physiological abilities to control salt and water balance in the laboratory, how do lugworms cope with the rigorous conditions of varying salinities in estuaries?

The actual tolerance of lugworms to low salinities may not be so great as generally believed. Table I gives a number of records of low salinity tolerances for 3 species of lugworms; undoubtedly other low salinity limits have been published, especially in faunal lists, but I hope that this selection is representative. Table I gives a first impression that lugworms can tolerate salinities down to at least 23‰ SW (8‰S) in the field, and much lower salinities in the laboratory. However, in the laboratory lugworms show obvious signs of injury when exposed to salinities below about 25‰ SW for more than a few hours. Schlieper's (1929) record for *A. marina* surviving 26 hours in 15‰ SW and Zenkevich's

(1938b) record for *Ad. branchialis* surviving 25 hours in 9‰ SW are by far the longest recorded laboratory survivals of lugworms in salinities below 23‰ SW. *Ab. pacifica* placed in salinities lower than about 50‰ SW recovered if returned to higher salinities within 1–2 days. Thus, in this species, brief exposures to low salinities do not cause irreversible damage.

A salinity of 5–8‰ is frequently regarded as representing an important boundary for the low salinity tolerance of euryhaline estuarine osmoconformers (review; Khlebovich, 1969). This critical low salinity limit was termed the “horohalinicum” by Kinne (1971). The horohalinicum is not a tolerance boundary for such estuarine worms as nereid polychaetes, but it seems significant that 5–8‰S is approximately the external concentration at which these worms abandon osmoconformity and begin to hyperosmoregulate (Oglesby, 1969a). The horohalinicum of natural waters seems to be characterized by marked changes in ion ratios, which are constant throughout the entire range of higher salinities. At and below the horohalinicum, K^+ and Ca^{++} tend to become much more abundant relative to Na^+ than in higher salinities (Khlebovich, 1969; Kinne, 1971). Thus, the several observations that lugworms can survive up to 2 days in salinities below 8‰ in the laboratory may be a fortunate consequence of the use of distilled water to make seawater dilutions, leaving the various ion ratios unaltered. However, for the osmoregulator *Nereis diversicolor*, Ca^{++} must be present in the external medium for survival in salinities below the horohalinicum (Oglesby, 1970; Smith, 1970).

While there are a number of references to lugworms being found exposed to salinities as low as 8‰ in the field (Table I), suggesting that lugworms can exist naturally down to the horohalinicum, many low salinity records seem to be of the type described by Nicol (1935). She states (page 220) that *A. marina* is “found in [salt marsh] pools of an average salinity as low as 15‰. In the pools the salinity does not often fall below 8‰.” Nicol’s observations may well be the actual basis for later undocumented and unqualified statements, such as that *A. marina* “can tolerate reduced salinities down to about 8‰” (Green, 1968) (e.g., also Krogh, 1939; Wells and Ledingham, 1940). Nicol clearly stated that these reductions of salinity were brief and temporary, due to rainfall or to surface runoff, and that they did not influence interstitial water salinity to any extent even when the salinity of the overlying water was considerably reduced.

That burrowing animals may be able to avoid or reduce contact with overlying waters of low salinity for short periods of time, while remaining in contact with interstitial water of much higher salinity, is discussed in some detail by Oglesby (1969b). Such burrowers will be limited by how long they can tolerate the absence of new water for burrow ventilation. In the case of lugworms, such periods may be quite long. May (1972, page 80) observed that *Ab. pacifica* “appeared healthy after three days in anoxia,” and Hecht (1932) maintained *A. marina* for 9 days in the absence of oxygen. Thus, lugworms are capable of “riding out” short periods of lowered environmental salinities in much the same way as can barnacles (Newman, 1967) and bivalve molluscs (Gilles, 1972), which prevent contact of the body with external medium by closing their shells. MacGinitie (1939), for example, reported that a number of soft-bodied burrowing invertebrates, including *A. brasiliensis* Nonato (as *A. cristata*), survived a major freshwater flood in the normally marine Newport Bay in southern California, while

epifaunal forms lacking shells were killed. Just how effectively a lugworm can plug its burrow against temporarily adverse environmental conditions is still a matter of controversy (Hoffman and Mangum, 1972; Vogel and Bretz, 1972).

Table I shows that with the exception of these questionable records for lugworms at 8‰S (23% SW), the lowest limit for worms in the field is considerably higher, from 41% SW (Reid, 1929) to 60–70% SW (Percival, 1929; Popham, 1966; this report). This high value for long-term survival of low salinities in the field is consistent with those few studies on long-term survival in the laboratory, and not inconsistent with observations that lugworms can survive temporary exposure to lower salinities both in the laboratory and in the field.

In the Coos Bay system (Fig. 1), as elsewhere (Hobson, 1967), *Ab. pacifica* is not found in such obviously unsuitable substrates as rocks, gravels, and coarse sand. It is often very abundant in finer sandy-muds with a moderate organic matter content. This distribution pattern seems typical of lugworms generally (*e.g.*, Longbottom, 1970), probably due to the similar feeding and burrowing mechanisms of all members of the family (Hobson, 1967). However, differences in details of substrate preference have been observed (Healy, 1963; Hobson, 1967) such that sympatric species are not usually found together. Sediments suitable for lugworms require calm waters and a depositional environment for development, and while such situations commonly occur in estuaries, lugworms can also be found along the open coast in situations in which wave action is much reduced (Wells, 1963). Thus, *Ab. pacifica* is present on the purely marine beach at Sunset Bay (Fig. 1), where there is almost no wave action and sediments are similar to those within Coos Bay. Suitable muddy-sand substrates are widespread in the Coos Bay system, and *Ab. pacifica* is present, and often abundant, in most such areas (Fig. 1). However, *Ab. pacifica* is absent from certain areas in Coos Bay which seemingly have an appropriate substrate (Fig. 1). There seem to be two major categories of intertidal areas lacking lugworms in Coos Bay: areas subject to severe human disturbance in the form of inputs of domestic and industrial wastes, (*e.g.*, paper pulp mills, log storage areas, commercial shipping docks, fish canneries, *etc.*), and areas receiving freshwater inflows, either year-round or seasonally.

With reference to pollution, of particular interest is the paper mill at mile marker 4 (Fig. 1), which discharges about 1.5 million gallons of wastes each day onto a broad intertidal flat (U. S. Department of the Interior, 1971). These wastes are a complex mixture of partially digested wood residues, including high concentrations of polysaccharides and lignins, and sulfite waste liquors with a variety of acidic sulfur compounds at a pH of 2.0–2.5. Within about 1000 m both upstream and downstream of the outfall plume there is little or no infaunal life on the mud-flats. However, *Ab. pacifica* approaches the outfall plume more closely than any other macroscopic invertebrate. In the area most seriously affected by sulfite waste liquor disposal, the only animals present were a few small lugworms. Fecal castings were sometimes observed immediately adjacent to places where H₂S bubbled out of the substrate upon agitation and where sulfur-oxidizing bacteria had formed large mold-like patches of colloidal elemental sulfur on the surface. Several reports indicate that lugworms are notably tolerant of sulfide (Clay, 1959; Hecht, 1932; Perkins and Abbott, 1972; Sveshnikov, 1963). Patel and Spencer (1963) found

that blood from *A. marina* contained an active catalyst of sulfide oxidation, an oxidation product of haemoglobin they termed the "brown pigment." Patel and Spencer concluded (page 174) that "The presence of free haemin in the blood, coupled with its autocatalytic production by sulphide must afford the animal considerable protection against the toxic effects of sulphide." In view of the high tolerance of *Ab. pacifica* to sulfide conditions in the outfall plume from this pulp mill, it seems likely that this protective role of the brown pigment is found in all lugworms.

The relationship of the distribution of *Ab. pacifica* to freshwater inflows in the Coos Bay system is shown most obviously by the fact that lugworms are generally absent from the mouths of small streams entering the Bay, such as in South and North Sloughs, Haynes and Kentuck Inlets, and the Sloughs near Cooston (Fig. 1). At their farthest penetration up these streams, lugworms were found only on muddy-sand banks at the sides of the stream channels, exposed to air at most low tides (Porch, 1970). Such worms would not be exposed to the lowest salinities present at such locations over a single tidal cycle (Nicol, 1935; Oglesby, 1969b). Because of their small watersheds, these small streams would not increase much in volume during the rainy season, and thus the lugworms on the side banks would probably not have to contend with much lower salinities during the winter than were observed in the summer.

At the mouth of the Coos River in the Bay (from mile markers 15-17 north to Cooston) there are extensive areas of intertidal mudflats which lacked lugworms. In summer 1970, interstitial salinities here were no lower than 28‰ (80‰ SW), even though lugworms were encountered elsewhere in the Bay in muds with interstitial salinities as low as 25‰ (71‰ SW). The Coos River itself has a variable flow, seldom exceeding 100 cubic feet per second during the dry season (May to October), but sometimes discharging as much as 1000 times more water during the rainy season (U. S. Department of the Interior, 1971). This intertidal area near the mouth of the river would be particularly subject to low salinities during periods of high river volume, and such periods may be expected to last many days to several weeks. At such times, interstitial salinities must surely drop to levels far lower than the low-salinity tolerance limits of *Ab. pacifica* (about 50‰ SW). The fact that *Nereis limnicola* is abundant in the area also suggests that these mudflats are exposed to low salinities for prolonged periods. *N. limnicola* is tolerant of low salinities and fresh water, and is usually restricted by interspecific competition to such habitats (Oglesby, 1965, 1968a; Smith, 1953). While settlement of lugworm larvae may possibly occur on these mudflats during the summer, young worms would be unlikely to survive lengthy low salinity conditions during the winter, and thus permanent populations could not become established.

It seems reasonable to conclude that lugworms are important members of the mudflat infauna only in those estuaries which are sufficiently dominated by the sea that interstitial salinities do not drop below about 50‰ SW, and where the salinity of the overlying water does not drop below this critical level for more than a few days. Thus, *Ab. pacifica* is one of the most widespread polychaetes in the Coos Bay system, not because it can osmoregulate or even tolerate salinities

below about 50% SW, but because most of the Coos Bay system is not exposed to lower salinities.

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SUMMARY

1. The lugworm *Abarenicola pacifica* can tolerate salinities as low as 23% SW in the laboratory, but is unlikely to survive more than brief exposure to salinities lower than 50% SW in the field.

2. Over this salinity range, *Ab. pacifica* is an osmotic conformer, but the coelomic fluids are slightly hyperosmotic to the medium. The literature suggests that other members of the family have a similar osmotic behavior.

3. At all salinities, the coelomic fluids of *Ab. pacifica* are slightly hypo-ionic to the medium with respect to Cl^- and Na^+ . Ion regulation appears to be very limited in all members of the family.

4. *Ab. pacifica* has very little ability to control its water content and volume in different salinities.

5. The relationship of the osmotic physiology of lugworms to their distribution in estuaries is discussed. While lugworms may be able to avoid contact with overlying waters of too low salinity for perhaps a few days, they are unlikely to form permanent populations in those parts of estuaries where the interstitial salinities drop below 50% SW during any part of the year.

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